



## A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century

J. Lenoir, *et al.*

*Science* **320**, 1768 (2008);

DOI: 10.1126/science.1156831

**The following resources related to this article are available online at  
[www.sciencemag.org](http://www.sciencemag.org) (this information is current as of July 27, 2008 ):**

**Updated information and services**, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/320/5884/1768>

**Supporting Online Material** can be found at:

<http://www.sciencemag.org/cgi/content/full/320/5884/1768/DC1>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/cgi/content/full/320/5884/1768#related-content>

This article **cites 29 articles**, 5 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/320/5884/1768#otherarticles>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

A. Hudson, S. Hunter-Smith, S. Kearney, L. Kimball, K. Rozofsky, J. Smith, and P. Tester provided assistance in the lab. Sequence accession numbers in GenBank are EU737149 to EU740386, EF521416 to EF521576, and EU302706 to EU302748.

**Supporting Online Material**  
www.sciencemag.org/cgi/content/full/320/5884/1763/DC1  
Materials and Methods  
SOM Text  
Figs. S1 to S3

Tables S1 to S3  
References

12 March 2008; accepted 29 May 2008  
10.1126/science.1157704

# A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century

J. Lenoir,<sup>1\*</sup> J. C. Gégout,<sup>1</sup> P. A. Marquet,<sup>2,3,4</sup> P. de Ruffray,<sup>5</sup> H. Brisse<sup>6</sup>

Spatial fingerprints of climate change on biotic communities are usually associated with changes in the distribution of species at their latitudinal or altitudinal extremes. By comparing the altitudinal distribution of 171 forest plant species between 1905 and 1985 and 1986 and 2005 along the entire elevation range (0 to 2600 meters above sea level) in west Europe, we show that climate warming has resulted in a significant upward shift in species optimum elevation averaging 29 meters per decade. The shift is larger for species restricted to mountain habitats and for grassy species, which are characterized by faster population turnover. Our study shows that climate change affects the spatial core of the distributional range of plant species, in addition to their distributional margins, as previously reported.

**R**ecent warming has induced biological and ecological responses from animals and plants throughout the world (1–3). Consistent responses to global warming or “fingerprints” are apparent in the phenology and distribution of species (1–5). For plants, invertebrates, and vertebrates, climate change has strongly influenced distribution and abundance at range margins both in latitude (polar margins) (5–8) and in elevation (upper margins) (5, 9–11), and even in depth for marine fishes (8). Shifts at the upper edge of altitudinal range agree with the hypothesis of an upward trend to escape rising temperatures (12–14). Changes in range limits, however, are just one, albeit important, expression of the likely consequences of climate change. More subtle changes within the ranges of species are also likely and, although poorly explored as yet, might have important ecological and evolutionary consequences. Assuming niche conservatism over evolutionary time (15), we tested for large-scale (across temperate and Mediterranean mountain forests in west Europe), long-term (over the 20th century), and multispecies (through an assem-

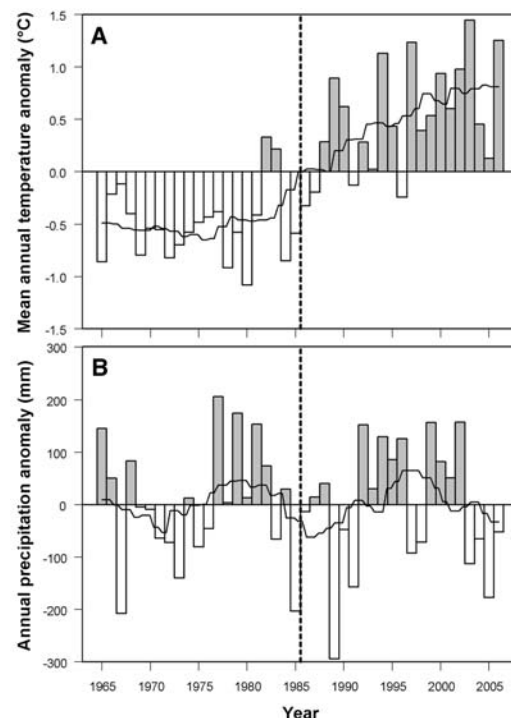
blage of 171 species) climate-related responses in forest plant altitudinal distributions. We analyzed species responses by measuring shifts in the altitudinal position of species' maximum probability of presence within their distribution, instead of focusing on distributional extremes. Additionally, we tested for the effect of ecological and life history traits on the magnitude of the response to climate warming (16). In particular, we tested whether species restricted to mountain areas

(10–12, 17, 18) and/or fast generation times (19) are particularly sensitive to temperature changes.

We studied species in forest communities found between lowland to the upper subalpine vegetation belt (0 to 2600 m above sea level) over six mountain ranges in west Europe (the Western Alps, the Northern Pyrenees, the Massif Central, the Western Jura, the Vosges, and the Corsican range). Climatic change in France has been characterized by increases in average temperature of far greater magnitude than increases in the world mean annual temperature, of about 0.6°C over the 20th century (20), reaching up to 0.9°C (21) and even close to 1°C in the alpine region since the early 1980s (22). From two large-scale floristic inventories (about 28,000 surveys) (23), we extracted two well-balanced subsamples, including 3991 surveys each, carried out across the studied mountain ranges (see fig. S1 for surveys location). The first subsample included surveys carried out before the mid-1980s (1905–1985), and the other one, after 1985 (1986–2005) (see fig. S2 for altitudinal distribution of surveys). We chose this temporal threshold because the analysis of yearly mean surface temperature anomalies between 1965 and 2005 shows that in 1986 the studied mountain ranges experienced a temperature regime shift (Fig. 1A), staying above the average baseline conditions. In contrast, analysis of annual precipitation anomalies between 1965

**Fig. 1.** Climatic trends from 1965 to 2006.

(A) Yearly mean surface temperature anomalies (using overall mean temperature as baseline) and (B) annual precipitation anomalies (using overall mean annual precipitation as baseline) averaged for 73 elevation sites in the French mountains ranging in altitude from 10 to 2010 m above sea level. Solid gray bars refer to positive anomalies, whereas open bars refer to negative ones. The solid curve is the smoothed average with use of a 10-year filter. The vertical dotted lines mark the split between the two studied periods. Data have been gathered from the French National Climatic Network (Météo-France).



<sup>1</sup>AgroParisTech, UMR 1092, Laboratoire d'Etude des Ressources Forêt-Bois (LERFoB), 14 rue Girardet, F-54000 Nancy, France.

<sup>2</sup>Center for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340 C.P. 6513677, Santiago, Chile. <sup>3</sup>Institute of Ecology and Biodiversity (IEB), Casilla 653, Santiago, Chile. <sup>4</sup>Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA. <sup>5</sup>CNRS, Institut de Biologie Moléculaire des Plantes (IBMP), Université Louis Pasteur, 12 Rue du Général Zimmer, F-67084 Strasbourg Cedex, France. <sup>6</sup>CNRS, UMR 6116, Institut Méditerranéen d'Ecologie et de Paléocécologie (IMEP), Faculté des Sciences de Saint Jérôme, case 461, F-134397 Marseille Cedex 20, France.

\*To whom correspondence should be addressed. E-mail: jonathan.lenoir@agroparistech.fr

and 2005 does not show any trend or precipitation regime shift (Fig. 1B). The subsampling method (23) was carried out in order to avoid a potential bias attributable to an uneven sampling effort between periods. In particular, we controlled for artificial warming (fig. S1) (23), which could be generated by the sampling of recent plots located in warmer conditions (i.e., southern latitude) regardless of climate warming. Our study was restricted to forest communities where long-term changes outweigh short-term tendencies because the forest canopy acts as a buffer zone, smoothing extreme interannual variation in temperature, in comparison with open areas that are far more influenced by both interannual climatic variation and agricultural practices. Changes in species distribution under the forest canopy can therefore be considered as fingerprints of regional trends rather than reflecting idiosyncratic trends in time or space.

Because we were more interested in the unexplored phenomenon of within-range shifts in plant species, we investigated changes in species optimum elevation over the study period instead of changes at the upper and lower boundaries of their distributions, which are more sensitive to sampling effort (24). By using simple logistic regression, we computed the altitude of maximum probability of presence, also called optimum

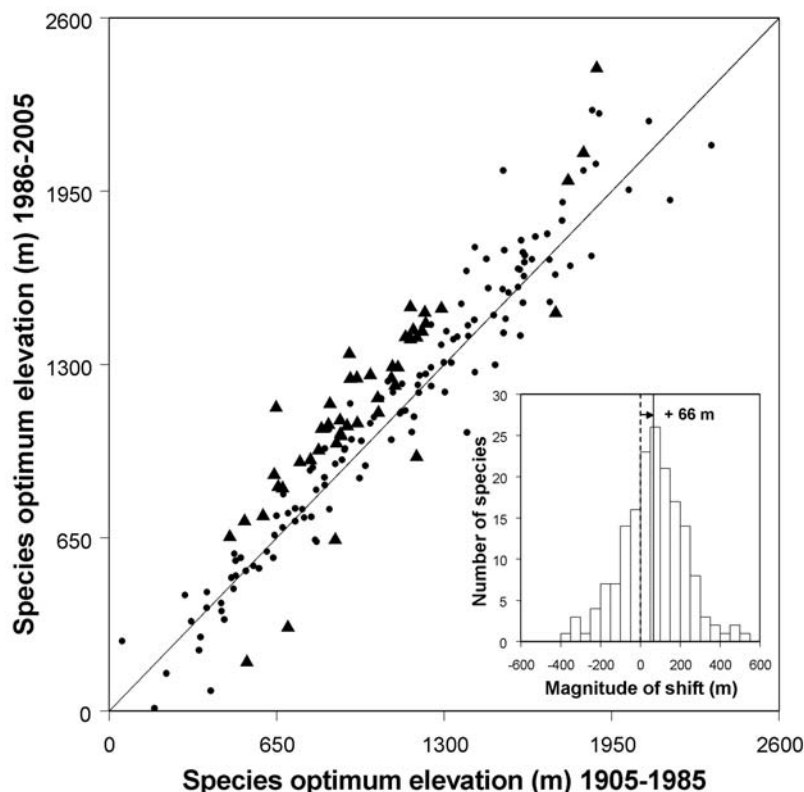
elevation, within each period for 171 species (table S2) that were best described by unimodal bell-shaped models (23) and had more than 50 occurrences (25). In total, the studied species account for almost 62% of occurrences in our data set. The change in the altitudinal distribution of species was measured as the difference in their optimum elevation between 1905–1985 and 1986–2005.

The optimum elevation of forest plant species shifted mostly upward during the end of the 20th century (Fig. 2). The general upward trend between 1971 (mean year of surveys occurring from 1905 to 1985) and 1993 (mean year of surveys occurring from 1986 to 2005) is statistically highly significant [mean difference in optimum elevation 64.8 m, 95% confidence interval (95% CI) for mean = 40.8, 88.8;  $n = 171$ ; Student's paired-sample  $t$  test,  $t = 5.33$ ;  $df = 170$ ;  $P < 10^{-4}$ ], amounting to an average of 29.4 m per decade. As a test of the robustness of the observed trend, we confirmed that the potential existence of an artifact in optimum elevation estimations because of the use of unimodal symmetric curves (26) did not account for the observed pattern of positive shifts in altitudinal distributions. Indeed, such potential artifacts should affect optimum elevation estimations regardless of the period, and thus no trend should be expected. Interestingly, the size of

the species altitudinal range around the optimum elevation (27) did not show a significant change between periods. The observed change in optimum elevation and lack of it in amplitude or range suggest that both the upper and the lower distributional margins may have shifted upward, implying the displacement of the whole altitudinal range.

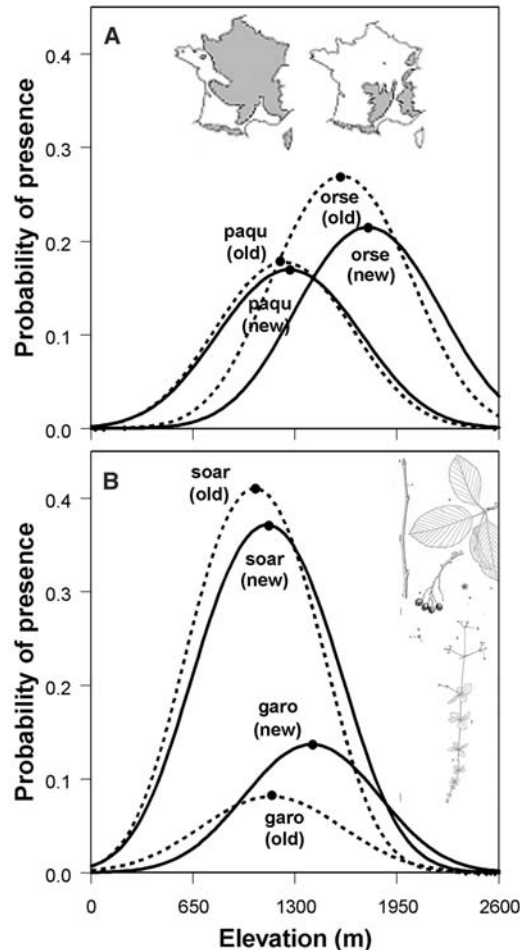
Most species in the 1986–2005 period had higher optimum elevations than those in the 1905–1985 period (Fig. 2). More than two-thirds (118/171) of the species shifted their optima upward, whereas only one-third (53/171) shifted their optima downward. Change in optimum elevation of any individual species or taxon may have a number of possible explanations, but confounding factors decline with increasing numbers of species studied (1). This overall upward trend for an assemblage of 171 forest plant species in western European mountains is consistent with results focusing on the highest alpine and nival vegetation belts (10–12, 28). We provide strong evidence that forest plant species, as many vertebrates and invertebrates species (8, 24, 29–31), have already followed the pace of climate change by shifting their distributions to higher altitudes and that these changes affect the core of their ranges or those areas where habitat suitability or maximum probability of presence is the highest. Thus, climate warming does not only affect species at their range boundaries, but its consequences ripple through the whole range of species.

In general, our results show that species displayed different rates of movement, behaving in a seemingly idiosyncratic way in response to climate change (Fig. 2 inset). However, species that share the same ecological properties may show similar consistent patterns of changes (32). We tested the hypothesis that species geographically restricted to mountains and/or with a shorter life cycle show more pronounced changes in distribution than those not restricted to mountain habitats and/or long-lived (23). Figure 3A illustrates a larger shift in the optimum elevation for the mountainous (area of occupancy restricted to mountain ranges) *Orthilia secunda* than for the ubiquitous (area of occupancy that encompassed both mountain ranges and lowland areas) *Paris quadrifolia*, whereas Fig. 3B illustrates a larger shift for the small grassy (associated with a fast breeding rate) *Galium rotundifolium* than for the large woody (associated with a slow breeding rate) *Sorbus aria* (see also tables S1 and S2). Overall, species that shifted the most are mountainous species as compared with ubiquitous species (Fig. 4) [one-way analysis of variance (ANOVA),  $F = 10.73$ ,  $n = 171$ ,  $df = 1$ ,  $P < 10^{-4}$ ]. Similarly, most shifting species tend to have life forms (herbs, ferns, and mosses) involving faster life history traits (shorter life cycle, faster maturation, and smaller sizes at maturity) than do species showing a reduced shift (trees and shrubs) (Fig. 4) (one-way ANOVA,  $F = 5.73$ ,  $n = 171$ ,  $df = 1$ ,  $P = 0.02$ ). Larger distributional shifts for faster life cycle species are consistent with results already observed in vertebrate taxa (8). Similarly, larger shifts for



**Fig. 2.** Scatter diagram of forest plant species ( $n = 171$ ) optimum elevation (i.e., altitude value at maximum probability of presence) for the periods 1905–1985 and 1986–2005. Each point represents one species: Species showing nonoverlapping 95% CIs around the optimum elevation between periods are displayed as solid triangles (▲) ( $n = 46$ ), whereas species with overlapping 95% CIs are displayed as solid circles (●) ( $n = 125$ ) (see tables S1 and S2 for details) (23). (Inset) The distribution of the species differences in optimum elevation between periods. The vertical dotted line marks zero shift, and the vertical solid line marks the median shift. The arrow describes the direction of the shift.

**Fig. 3.** Examples of western European plant distributions that have shifted upward. Elevational response curves derived with logistic regression models during 1905–1985 (dotted lines) and during 1986–2005 (solid lines) for two species according to geographic distribution pattern (A), ubiquitous *P. quadrifolia* (paqu) and mountainous *O. secunda* (orse), and also for two species according to life form (B), grassy *G. rotundifolium* (garo) and woody *S. aria* (soar). The solid circles (●) indicate the position of the optimum elevation. Maps and drawing pictures (D. Mansion) are from the Flore Forestière Française Sources (Institut pour le Développement Forestier).

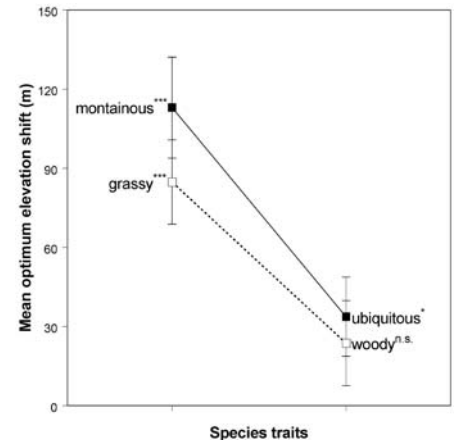


mountainous species are in agreement with the suggestion that plant species would be more sensitive to climate change at high-altitude locations (10, 11, 17). There is no significant interaction between geographic distribution pattern and life form (two-way ANOVA,  $F=0.24$ ,  $n=171$ ,  $df=1$ ,  $P=0.63$ ), which rules out the possibility that forest plant species restricted to mountains show larger changes because most of them exhibit a grassy life form.

Recent meta-analyses have conclusively showed the response of species to climate change (1, 3, 5). However, little is known regarding how climate change interplay with other regional- to global-scale drivers of changes in affecting species distributions such as variation in precipitation regime, nitrogen (N) deposition, land-use changes, invasive species, and  $\text{CO}_2$  increases. Decadal-scale variation in precipitation has remained the same before and after the slicing of our studied period (Fig. 1B); thus, it cannot directly affect the distributional changes we observed. Atmospheric N deposition are important at high elevations, with rates ranging from 6 to 30  $\text{kg ha}^{-1} \text{ year}^{-1}$  in western European mountains (33). However, we found a slightly lesser but not significant N demand (23) for upward-shifting species as compared with those shifting downward (mean N demands for upward and downward species were

4.38 and 4.97, respectively; Student's two-sample  $t$  test,  $t=1.72$ ;  $n=127$ ;  $df=125$ ;  $P=0.09$ ); hence, N deposition did not explain the general upward shift. The effect of land-use changes can also be ruled out because we paid particular attention to restricting our analysis to mature forests (23), where land-use changes are of reduced magnitude. Lastly, neither invasive species introduction nor changing concentration of atmospheric  $\text{CO}_2$  seem to be important in determining the observed regional pattern of positive shifts in altitudinal distributions; if present, no significant trend in altitudinal shift would be expected because these drivers are nondirectional regarding species responses and would affect as many increases as decreases.

The average magnitude of change in forest plant species optimum elevation across the entire altitudinal gradient [ $29.4 \pm 10.9$  m per decade (23)] closely matches the figure observed for the shift of alpine plants above the tree line [ $27.8 \pm 14.6$  m per decade (12)] and even improves the precision. Further, if we assume a temperature lapse rate of  $0.6^\circ\text{C}$ , our results imply a  $0.39^\circ\text{C}$  increase in 22 years, which is coherent with the observed warming trend, supporting the hypothesis that climate warming is the main driving force for the observed patterns. The wide variability in the magnitude of optimum elevation shifts



**Fig. 4.** Magnitude of optimum elevation shifts for plant species in relation to their ecological and life history traits (23). Shifts in mean optimum elevation according to geographic distribution pattern (solid line and symbols) correspond to ubiquitous ( $n=104$ ), and mountainous species ( $n=67$ ). Shifts in mean optimum elevation according to life form (dotted line and open symbols) correspond to woody ( $n=56$ ) and grassy species ( $n=115$ ). Means are shown with standard errors. Significance of the magnitude of mean shift from the null hypothesis of zero shift is displayed for each trait (n.s. indicates nonsignificant,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ; Student's paired sample  $t$  test).

among species within assemblages may likely result in the disruption of biotic interactions and the ecological networks wherein these species are embedded. Further studies aimed at disentangling the magnitude and consequences of these changes, and their impact on species persistence and ecosystem functioning, are urgently needed.

#### References and Notes

1. C. Parmesan, G. Yohe, *Nature* **421**, 37 (2003).
2. G. R. Walther *et al.*, *Nature* **416**, 389 (2002).
3. T. L. Root *et al.*, *Nature* **421**, 57 (2003).
4. L. Hughes, *Trends Ecol. Evol.* **15**, 56 (2000).
5. R. Hickling, D. B. Roy, J. K. Hill, R. Fox, C. D. Thomas, *Glob. Change Biol.* **12**, 450 (2006).
6. M. Sturm, C. Racine, K. Tape, *Nature* **411**, 546 (2001).
7. F. S. Chapin III *et al.*, *Ambio* **33**, 361 (2004).
8. A. L. Perry, P. J. Low, J. R. Ellis, J. D. Reynolds, *Science* **308**, 1912 (2005); published online 12 May 2005 (10.1126/science.1111322).
9. P. Tryjanowski, T. H. Sparks, P. Profus, *Divers. Distrib.* **11**, 219 (2005).
10. F. Keller, F. Kienast, M. Beniston, *Reg. Environ. Change* **1**, 70 (2000).
11. G. Grabherr, M. Gottfried, H. Pauli, *Nature* **369**, 448 (1994).
12. G. R. Walther, S. Beibner, C. A. Burga, *J. Veg. Sci.* **16**, 541 (2005).
13. J. Penuelas, M. Boada, *Glob. Change Biol.* **9**, 131 (2003).
14. L. Kullman, *J. Ecol.* **90**, 68 (2002).
15. A. T. Peterson, J. Soberon, V. Sanchez-Cordero, *Science* **285**, 1265 (1999).
16. S. Lavergne, J. Molina, M. Debussche, *Glob. Change Biol.* **12**, 1466 (2006).
17. H. Pauli, M. Gottfried, K. Reiter, C. Klettner, G. Grabherr, *Glob. Change Biol.* **13**, 147 (2007).
18. W. Thuiller, S. Lavorel, M. B. Araujo, M. T. Sykes, I. C. Prentice, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 8245 (2005).



19. M. Cardillo *et al.*, *Science* **309**, 1239 (2005).
20. P. D. Jones, T. J. Osborn, K. R. Briffa, *Science* **292**, 662 (2001).
21. J. M. Moisselin, M. Schneider, C. Canellas, O. Mestre, *Meteorologie* **38**, 45 (2002).
22. M. Beniston, H. F. Diaz, R. S. Bradley, *Clim. Change* **36**, 233 (1997).
23. Materials and methods are available as supporting material on Science Online.
24. L. P. Shoo, S. E. Williams, J. M. Hero, *Austral Ecol.* **31**, 22 (2006).
25. C. Coudun, J.-C. Gégout, *Ecol. Modell.* **199**, 164 (2006).
26. The impact of the symmetry assumption in Gaussian logistic regressions (GLR) on our results was tested by using a more flexible curve-fitting tool, namely generalized additive models (GAM), which allows for asymmetry in hump-shaped curves (23). We also found a statistically highly significant shift of 27 m per decade (mean difference in optimum elevation 59.4 m, 95% CI = 16.5, 102.4;  $n = 171$ ; Student's paired-sample  $t$  test,  $t = 2.73$ ;  $df = 170$ ;  $P < 10^{-2}$ ).
27. The ecological amplitude is a proxy for the size of the species altitudinal range around the optimum elevation (23). We found no significant differences between 1905–1985 and 1986–2005 (mean difference in ecological amplitude 2.3 m, 95% CI = -11.9, 16.6;  $n = 171$ ; Student's paired-sample  $t$  test,  $t = 0.32$ ;  $df = 170$ ;  $P = 0.75$ ).
28. P. Lesica, B. McCune, *J. Veg. Sci.* **15**, 679 (2004).
29. R. J. Wilson *et al.*, *Ecol. Lett.* **8**, 1138 (2005).
30. M. Konvicka, M. Maradova, J. Benes, Z. Fric, P. Kepka, *Glob. Ecol. Biogeogr.* **12**, 403 (2003).
31. J. K. Hill *et al.*, *Proc. R. Soc. London Ser. B* **269**, 2163 (2002).
32. W. Thuiller, S. Lavorel, M. B. Araujo, *Glob. Ecol. Biogeogr.* **14**, 347 (2005).
33. E. Dambrine *et al.*, in *Forest Decline and Atmospheric Deposition Effects in the French Mountains*, G. Landmann, M. Bonneau, Eds. (Springer Verlag, Berlin, 1994), pp. 177–200.
34. We thank the thousand of recorders who contributed to the building of EcoPlant and Sophy databases; J.-D. Bontemps, J.-C. Pierrat, and C. Coudun for their much-appreciated statistical advice; J.-L. Dupouey for stimulating discussion; and three anonymous reviewers for helpful comments on previous versions of this manuscript that strongly improved the quality of our

analyses. EcoPlant is a phytocological database financed by the French Environment and Energy Management Agency (ADEME) and the Office National des Forêts (ONF). Part of this work was conducted while P.A.M. was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a center funded by NSF (grant DEB-0072909), the University of California, and the Santa Barbara campus. P.A.M. acknowledges support from a Guggenheim Fellowship and grants FONDAP-FONDECYT 1501-0001 and ICM P05-02 PFB-23 CONICYT. J.C.G. acknowledges support from FONDECYT 11060313 and FONDECYT Cooperacion Internacional 7070147. J.L. was found by a Ph.D. grant from the French National Institute for Agricultural Research (INRA).

#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/320/5884/1768/DC1](http://www.sciencemag.org/cgi/content/full/320/5884/1768/DC1)  
Materials and Methods  
Figs. S1 and S2  
Tables S1 and S2  
References

21 February 2008; accepted 22 May 2008  
10.1126/science.1156831

# Polarization of the *C. elegans* Embryo by RhoGAP-Mediated Exclusion of PAR-6 from Cell Contacts

Dorian C. Anderson, Jason S. Gill,\* Ryan M. Cinalli,\* Jeremy Nance†

Early embryos of some metazoans polarize radially to facilitate critical patterning events such as gastrulation and asymmetric cell division; however, little is known about how radial polarity is established. Early embryos of *Caenorhabditis elegans* polarize radially when cell contacts restrict the polarity protein PAR-6 to contact-free cell surfaces, where PAR-6 regulates gastrulation movements. We have identified a Rho guanosine triphosphatase activating protein (RhoGAP), PAC-1, which mediates *C. elegans* radial polarity and gastrulation by excluding PAR-6 from contacted cell surfaces. We show that PAC-1 is recruited to cell contacts, and we suggest that PAC-1 controls radial polarity by restricting active CDC-42 to contact-free surfaces, where CDC-42 binds and recruits PAR-6. Thus, PAC-1 provides a dynamic molecular link between cell contacts and PAR proteins that polarizes embryos radially.

Early embryos can polarize radially when cell contacts differentiate the contacted (inner) and contact-free (outer) surfaces of each cell. Radial polarity, called compaction in mammals, provides a foundation for executing critical patterning events such as cell fate specification and gastrulation (1, 2). For example, radial polarity in *Caenorhabditis elegans* allows gastrulating cells to enrich myosin at their outer surfaces; myosin constricts these surfaces to help drive gastrulating cells into the embryo (2, 3). The *C. elegans* embryo polarizes radially when cell contacts restrict the polarity proteins PAR-6 [PSD-95/DLG/ZO-1 (PDZ) and semi-Cdc42/Rac-interactive-binding (semi-CRIB) domain protein], PAR-3 (PDZ domain protein), and PKC-3 (atypical protein kinase C) to the outer surfaces of early embryonic somatic cells (EES cells) (2, 4–6). This “inner-outer”

PAR asymmetry begins at the four-cell stage and persists through early embryogenesis (6). The molecular link between cell contacts and the inner-outer PAR asymmetries they induce to polarize embryos is not known.

To learn how radial polarity is established, we screened for mutations preventing the inner-outer asymmetry of green fluorescent protein (GFP)-tagged PAR-6 (PAR-6-GFP). Two mutations (*xn1* and *xn6*) in a gene we named *pac-1* (PAR-6-at-contacts) caused PAR-6-GFP to associate with both inner and outer surfaces of EES cells (Fig. 1, A and B). *pac-1* mutations are maternal-effect, and hereafter we refer to embryos produced by *pac-1*(*xn6*) mutant mothers as *pac-1* embryos.

We immunostained *pac-1* embryos to examine the localization of endogenous PAR proteins. PAR-6, PAR-3, and PKC-3 are restricted to outer surfaces of wild-type EES cells, but each protein showed a symmetric cortical localization in *pac-1* EES cells (Fig. 1, C to H, and table S2). PAR proteins within the zygote and germline precursor cell of wild-type early embryos develop anterior-posterior (A/P) asymmetries that are not patterned

strictly by cell contacts. These PAR asymmetries appeared normal in *pac-1* embryos (fig. S1). *pac-1* mutations also did not disrupt PAR-6 asymmetry in epithelial cells, which are born at later stages and localize PAR-6 apically (7). Thus, *pac-1* is essential for contact-mediated PAR asymmetries that develop during radial polarization but appears dispensable for other types of PAR asymmetries.

Depleting PAR-6 or PAR-3 specifically from EES cells causes slowed gastrulation (2). In wild-type embryos, gastrulation begins when the two endodermal precursor cells (EPCs) ingress into the interior. We filmed *pac-1* embryos to determine whether loss of inner-outer PAR asymmetry also disrupts gastrulation. EPCs ingressed significantly more slowly in *pac-1* embryos (8) and were often present on the surface at a time that they would be internalized in wild type (Fig. 2, A and B, movies S1 and S2). Similar to embryos lacking PAR-3 or PAR-6 in EES cells (2), the slowed cell ingressions in *pac-1* embryos did not prevent EPC descendants from ultimately internalizing, and embryos were viable.

PAR-3 is required for nonmuscle myosin to concentrate at and constrict the EPC outer surfaces (2, 3). To determine whether the gastrulation defects we detected might be explained by altered myosin localization or activity, we immunostained embryos for activated myosin regulatory light chain (p-rMLC) (9). In wild type, p-rMLC concentrated at outer surfaces of ingressing EPCs, similar to published reports (Fig. 2C) (9). By contrast, levels of p-rMLC at outer surfaces of *pac-1* EPCs were reduced significantly (Fig. 2D and fig. S2). These data suggest that PAC-1 regulates gastrulation by restricting PAR-3 to the outer cortex, where PAR-3 is needed to concentrate active myosin.

We cloned the *pac-1* gene (8), which encodes a protein containing a pleckstrin homology (PH) and a RhoGAP domain (Fig. 3A and fig. S3A). RhoGAP domains inhibit Rho guanosine triphosphatase (GTPase) signaling by converting active guanosine triphosphate-bound Rho proteins to inactive guanosine diphosphate-bound forms (10).

Kimmel Center for Biology and Medicine of the Skirball Institute, New York University School of Medicine, 540 First Avenue, New York, NY 10016, USA.

\*These authors contributed equally to this work.

†To whom correspondence should be addressed. E-mail: nance@saturn.med.nyu.edu



Supporting Online Material for

**A Significant Upward Shift in Plant Species Optimum Elevation During  
the 20th Century**

J. Lenoir,\* J. C. Gégout, P. A. Marquet, P. de Ruffray, H. Brisse

\*To whom correspondence should be addressed. E-mail: [Lenoir@Engref.Fr](mailto:Lenoir@Engref.Fr)

Published 27 June 2008, *Science* **320**, 1768 (2008)  
DOI: 10.1126/science.1156831

**This PDF file includes:**

Materials and Methods  
Figs. S1 and S2  
Tables S1 and S2  
References

## Supporting Online Material

### Materials and Methods

#### Collecting and extracting data

Complete species lists (presence/absence information) consistent with current floristic inventory practices (encompassing an area of 400 m<sup>2</sup>) were collated from two French databases, providing a total of 28,494 field forest floristic surveys. The first one, EcoPlant (*S1*), is a forest phytoecological database now integrating more than 120 different forest survey sources from the last century (1905-2005). The second one, Sophy (*S2*), is a phytosociological database now including approximately 2,500 different survey sources (forests and open landscapes) from the last century (1915-2000). To analyze climate change effect over the 20<sup>th</sup> century, we subsampled two data subsets from these databases, before and after 1985 as the warmest records were measured since the late 1980s (*S3*) and according to the temperature trend observed in the studied mountains (Fig. 1). Surveys too close in location (i.e. within a 500 m radius), and displaying similar ecological conditions, were removed to minimize spatial correlation and overweighing effects. We also paid particular attention to keep surveys in forest biomes and mature stands between our periods so as to avoid land-use issues by removing surveys carried out in dynamic forest stages (e.g. fallow land, moor and early stages of secondary succession). Once we had split the 1905-2005 time range, reduced spatial autocorrelation effects, and removed land-use issues, we identified surveys across the Western Alps, the Northern Pyrénées, the Massif Central, the Western Jura, the Vosges and the Corsican range during 1905-1985 (4,979 surveys) and also during 1986-2005 (6,482 surveys). To control for artificial warming (i.e. sampling

warmer conditions during 1986-2005), we balanced our two data subsets using the same temperature reference to compare equivalent spatial conditions for temperature (spatial control for temperature) regardless of temperature increases in time (temporal warming). Mean annual temperature (MAT) obtained from the meteorological model Aurelhy (S5) based on interpolated measurements from 1961-1990 observed data, was used as temperature reference. The position of all 11,461 selected surveys (regardless of period) was known with a precision of 1 km and MAT was available as a layer with 1 km<sup>2</sup> resolution in a GIS that covers the whole of France. Once we had extracted MAT for all 11,461 selected surveys from the GIS data layer, we balanced the number of surveys in both periods (uniform random selection) for each mountain ranges and every 1°C across the French MAT gradient. This procedure ensures equivalent average temperature conditions in space between 1905-1985 and 1986-2005 within each of the six studied mountain ranges, preventing potential biases attributable to spatial sampling effects rather than the studied temporal warming (mean MAT during 1905-1985 and 1986-2005 periods were: 9.206 and 9.208 °C respectively, Student's two-sample *t*-test,  $t = 0.04$ , degrees of freedom, d.f. = 7,98,  $P = 0.97$ ). After selection, we kept 7,982 surveys for analysis (Fig. S1): 3,991 forest sites for the 1905-1985 period (mean year of sampling: 1971) and 3,991 forest sites for the 1986-2005 period (mean year of sampling: 1993).

### **Monitoring changes in altitudinal position**

We determined the ecological response of each plant species to elevation in each period using simple logistic regression models and response curves (S6). Logistic regression is a generalised linear modelling technique (S7) using a logit link function



computed with the log-likelihood expression of a Bernoulli distribution (presence/absence) and is the method most often used to characterise species-environment relationships when presence/absence data is available. We characterised the significance of the Gaussian logit model (i.e. a positive effect of elevation and a negative effect of elevation<sup>2</sup> displaying a unimodal bell-shaped response curve) against the linear logit model (i.e. a positive or a negative effect of elevation displaying an increasing or decreasing sigmoidal response curve) and/or against the null model (i.e. no effect of elevation displaying a flat response curve) with a residual deviance test based on a Chi-squared distribution (S7). We used the drop in residual deviance as an index of the quality of species response along the altitudinal gradient. To track changes in altitudinal position, we compared the optimum information criterion (OPT) between periods. We also computed the tolerance information criterion as an estimation of the species ecological amplitude (AMP) or amplitude of the spatial distribution along the gradient. These Gaussian parameters can be easily found by the following formula (S8):

$$OPT = -\frac{b_1}{2b_2}$$

$$AMP = \frac{1}{\sqrt{-2b_2}}$$

where  $b_1$  and  $b_2$  are the two coefficients of the Gaussian logit model. OPT is an indicator of the species elevation preference, and represents the elevation value at which the probability of presence reaches its maximum (i.e. conditions at which growth and reproduction are the most favourable). Optimum elevation change for species should be

more indicative of a population response than change measured at range boundaries (*S4*). AMP is a proxy for the altitudinal range over which species can survive and reproduce. Ecological amplitude is not computed to analyze change at margins but to look for expansion (increasing ecological amplitude) or retraction (decreasing ecological amplitude) processes.

### **Species level statistical analysis**

To be included into the analyses, forest vegetation species (mosses, ferns, herbs, shrubs and trees) had to be present at least 50 times (*S9*) and display a highly significant Gaussian logit model (at the 0.001 level, Chi-squared test on the drop in residual deviance (*S7*)) along the altitudinal gradient at both periods (See Table S1 for the selected species list), which allowed us to compute an optimum within species elevation range in each periodic data set ( $n = 171$ ). Among the 2,853 species present in our data, the 171 studied species represented 62% of the data set total occurrences. This selection procedure ensured a good estimation of the overall shift in optimum elevation between periods, even if there is, at the species level, a potential artefact in optimum estimation due to the use of unimodal symmetric curves (*S10*). To test the hypothesis that the overall shift in optimum elevation was not an artefact resulting from the symmetry assumption made by the Gaussian logit model, we also used Generalized Additive Models (GAM) rendering asymmetry with a restricted cubic spline smoother (d.f. = 4) (*S11*) to determine the shape of response curves for the 171 studied species. For GAM, the optimum elevation along the altitudinal gradient was measured as the altitude where the species probability of presence reached the maximum. We also computed a 95% confidence interval for optimum elevation (*S12*) at

both periods (Table S2) to identify which species showed a significant shift (i.e. had non-overlapping 95% confidence interval between periods).

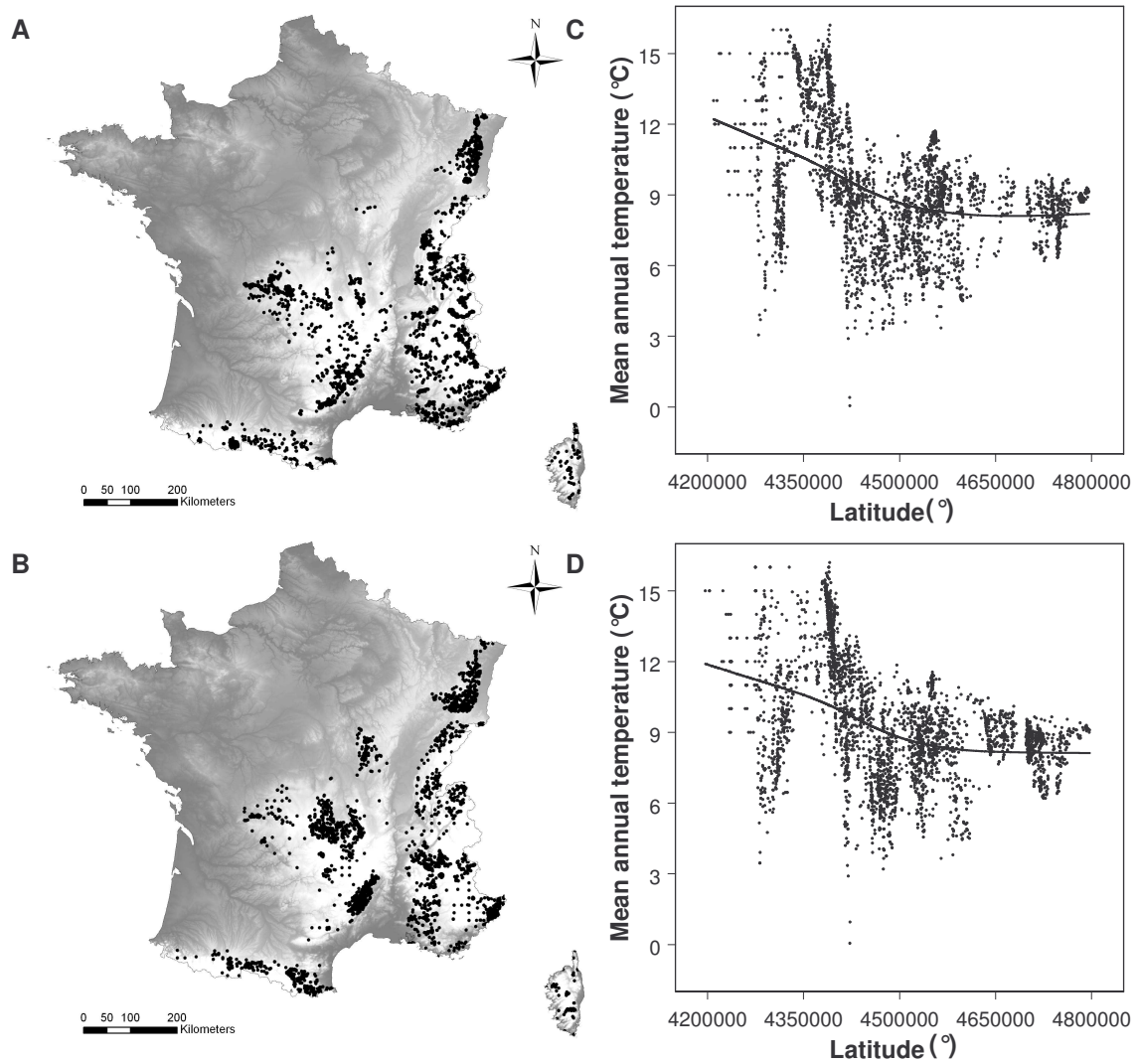
For each species, we compiled information about species geographic distribution pattern according to their ecological specificity for mountain ranges occurring in West Europe, and also information about species life-form according to their biological characteristics such as plant growth form (Table S1). We distinguished ‘mountainous’ species (*S13*, *S14*) displaying area of occupancy restricted to mountain ranges and vicinities ( $n = 67$ ), from ‘ubiquitous’ species (*S13*, *S14*) displaying area of occupancy not restricted to mountains but also found in plains and lowlands ( $n = 104$ ). We also assigned two different levels of life-forms using Raunkiaer’s classification (*S13*, *S14*) distinguishing the so called ‘grassy’ species (i.e. herbs, ferns and mosses) ( $n = 115$ ), and the so called ‘woody’ species (i.e. trees and shrubs) ( $n = 56$ ). In order to examine the effect of these traits upon changes in optimum elevation over time, we used One-way and Two-way layout Analysis of Variance (ANOVA) with a replicated factorial feature. Thus, we fitted species optimum differences as dependant variable, against species geographic distribution pattern and life-form as independent factors.

To determine whether the magnitude of shift in species altitudinal distribution was influenced by atmospheric nitrogen (N) deposition, Ellenberg indicator values (*S15*) were tabulated for the 171 studied species. We used Ellenberg N variable, a proxy of species N demand, ranging from 1 (species most frequent on soils extremely N deficient) to 9 (species most frequent on soils extremely rich in N). Because Ellenberg indicator values have not been published for all of the 171 species recorded, the number of species was 127.

Assuming the niche conservation hypothesis, an impact of N deposition on species optimum elevation can only occur with a gradient of N deposition along the altitudinal gradient, leading to a shift towards altitude with larger N deposition for N-rich-demanding species (i.e. species with high values of Ellenberg N variable) and towards altitude with lower N deposition for N-poor-demanding species (i.e. species with low values of Ellenberg N variable). All computations were performed with the 'S-plus 2000 professional release 3' statistical package.

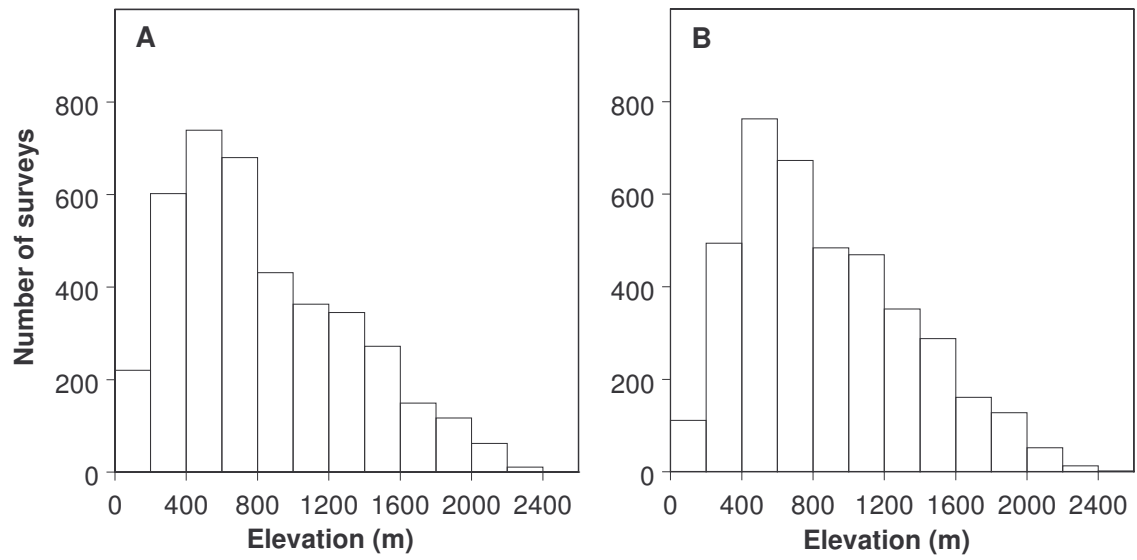
## Figures

**Figure S1.** Location of the 7,982 forest sites in Western European mountains during (A) 1905-1985 and (B) 1986-2005. Evolution of mean annual temperature of sampled surveys along the latitudinal gradient (WGS84) during (C) 1905-1985 and (D) 1986-2005. Solid curves have been smoothed using a smoothing spline (d.f. = 3). Mean annual temperatures were obtained from the meteorological model Aurelhy based on interpolated data gathered from the French National Climatic Network (Météo-France) during 1961-1990.





**Figure S2.** Altitudinal distribution of surveys in 200 m intervals during **(A)** 1905-1985 and **(B)** 1986-2005.



## Tables

**Table S1.** Species list displaying a highly significant Gaussian logit model (at the 0.001 level, Chi-squared test on the drop in residual deviance ( $D_0-D$ ) (S7)) within their elevation range for both periods (1905-1985 and 1986-2005).  $D_0$  is the null deviance, and  $D$  is the residual deviance of the Gaussian logit model. Species nomenclature followed Flora Europaea (S16).

Species	Range area	Life-form	1905-1985		1986-2005	
			$D_0$	$D_0-D$	$D_0$	$D_0-D$
<i>Abies alba</i>	mountainous	woody	4 719	400.44	5 237	802.78
<i>Acer campestre</i>	ubiquitous	woody	2 933	139.19	2 660	171.77
<i>Acer monspessulanum</i>	ubiquitous	woody	1 522	153.74	845	57.57
<i>Acer opalus</i>	mountainous	woody	2 492	124.91	2 469	112.64
<i>Acer platanoides</i>	ubiquitous	woody	927	42.16	1 193	28.27
<i>Acer pseudoplatanus</i>	ubiquitous	woody	3 050	110.00	3 663	155.80
<i>Actaea spicata</i>	mountainous	grassy	1 028	113.01	1 298	197.03
<i>Adenostyles alliariae</i>	mountainous	grassy	845	133.67	1 381	281.86
<i>Anemone nemorosa</i>	ubiquitous	grassy	2 267	24.02	2 442	28.56
<i>Anthyllis vulneraria</i>	ubiquitous	grassy	705	54.64	776	53.17
<i>Aquilegia vulgaris</i>	ubiquitous	grassy	1 166	57.00	776	72.63
<i>Arabis turrita</i>	mountainous	grassy	606	47.56	697	17.87
<i>Aruncus dioicus</i>	mountainous	grassy	631	74.10	614	60.04
<i>Aster bellidiastrum</i>	mountainous	grassy	753	168.00	721	210.85
<i>Athyrium filix-femina</i>	ubiquitous	grassy	3 368	123.88	3 609	116.80
<i>Atrichum undulatum</i>	ubiquitous	grassy	639	32.43	1 381	53.62
<i>Berberis vulgaris</i>	ubiquitous	woody	1 063	113.76	776	86.22
<i>Blechnum spicant</i>	ubiquitous	grassy	1 304	39.09	845	17.62
<i>Buxus sempervirens</i>	ubiquitous	woody	2 965	288.82	2 386	41.64
<i>Calamagrostis varia</i>	mountainous	grassy	868	191.75	776	137.86
<i>Calamintha grandiflora</i>	mountainous	grassy	1 014	214.00	1 498	393.11
<i>Campanula rhomboidalis</i>	mountainous	grassy	664	153.30	598	141.84
<i>Campanula rotundifolia</i>	ubiquitous	grassy	1 492	176.30	1 049	67.99
<i>Cardamine heptaphylla</i>	mountainous	grassy	1 564	164.91	1 709	226.35
<i>Cardamine pentaphyllos</i>	mountainous	grassy	697	76.99	876	179.91
<i>Cardamine pratensis</i>	ubiquitous	grassy	537	42.80	927	50.17
<i>Carex digitata</i>	ubiquitous	grassy	1 725	35.63	1 504	60.63
<i>Carex sylvatica</i>	ubiquitous	grassy	1 939	24.41	1 820	54.86
<i>Carpinus betulus</i>	ubiquitous	woody	2 258	345.43	2 487	495.57
<i>Castanea sativa</i>	ubiquitous	woody	2 832	451.93	3 233	470.21
<i>Cephalanthera longifolia</i>	ubiquitous	grassy	1 063	21.47	1 160	49.38
<i>Cephalanthera rubra</i>	ubiquitous	grassy	1 387	28.83	807	26.47
<i>Cicerbita alpina</i>	mountainous	grassy	581	103.71	631	109.68
<i>Clinopodium vulgare</i>	ubiquitous	grassy	2 038	56.63	1 976	93.67
<i>Corylus avellana</i>	ubiquitous	woody	4 480	202.33	4 394	257.67
<i>Crataegus laevigata</i>	ubiquitous	woody	721	33.63	1 119	88.80
<i>Crataegus monogyna</i>	ubiquitous	woody	4 013	320.85	3 866	250.24
<i>Cruciata glabra</i>	mountainous	grassy	978	93.30	913	57.84

Species	Range area	Life-form	1905-1985		1986-2005	
			D <sub>0</sub>	D <sub>0</sub> -D	D <sub>0</sub>	D <sub>0</sub> -D
<i>Cytisophyllum sessilifolium</i>	mountainous	woody	2 460	68.31	2 405	15.42
<i>Cytisus scoparius</i>	ubiquitous	woody	2 243	136.84	2 586	272.21
<i>Dactylorhiza maculata</i>	ubiquitous	grassy	745	37.72	1 000	101.02
<i>Daphne laureola</i>	ubiquitous	woody	2 140	65.38	2 400	94.10
<i>Digitalis lutea</i>	ubiquitous	grassy	1 146	18.36	1 206	27.77
<i>Digitalis purpurea</i>	ubiquitous	grassy	1 842	80.52	1 298	43.86
<i>Dryopteris dilatata</i>	ubiquitous	grassy	1 587	74.36	2 432	121.99
<i>Dryopteris filix-mas</i>	ubiquitous	grassy	3 722	110.92	4 211	212.64
<i>Epilobium angustifolium</i>	ubiquitous	grassy	1 324	162.60	1 355	122.79
<i>Epilobium montanum</i>	ubiquitous	grassy	2 660	168.12	2 766	327.45
<i>Epipactis atrorubens</i>	ubiquitous	grassy	1 084	98.88	729	96.87
<i>Epipactis helleborine</i>	ubiquitous	grassy	1 798	22.81	1 837	26.77
<i>Euphorbia characias</i>	ubiquitous	grassy	1 146	190.11	898	120.77
<i>Evonymus europaeus</i>	ubiquitous	woody	1 239	144.73	1 014	121.62
<i>Fagus sylvatica</i>	ubiquitous	woody	5 487	713.24	5 477	655.74
<i>Festuca altissima</i>	mountainous	grassy	2 175	129.18	2 054	119.75
<i>Festuca flavescens</i>	mountainous	grassy	905	326.14	1 285	502.19
<i>Festuca heterophylla</i>	ubiquitous	grassy	1 928	53.95	2 651	77.54
<i>Fragaria vesca</i>	ubiquitous	grassy	4 051	141.47	3 963	107.42
<i>Fraxinus excelsior</i>	ubiquitous	woody	3 531	136.73	3 926	167.50
<i>Galeopsis tetrahit</i>	ubiquitous	grassy	1 896	43.26	1 847	65.74
<i>Galium odoratum</i>	ubiquitous	grassy	3 481	335.48	3 816	353.83
<i>Galium rotundifolium</i>	mountainous	grassy	1 418	69.38	1 742	186.10
<i>Galium saxatile</i>	ubiquitous	grassy	1 132	62.29	898	80.07
<i>Genista cinerea</i>	mountainous	woody	664	47.45	1 014	18.53
<i>Genista pilosa</i>	ubiquitous	woody	1 837	38.56	1 399	38.21
<i>Gentiana lutea</i>	mountainous	grassy	1 056	244.82	1 035	333.90
<i>Geranium nodosum</i>	mountainous	grassy	1 213	17.69	1 720	170.25
<i>Geranium robertianum</i>	ubiquitous	grassy	3 119	94.17	3 077	115.97
<i>Gymnocarpium dryopteris</i>	mountainous	grassy	1 180	180.63	713	92.06
<i>Hedera helix</i>	ubiquitous	woody	4 802	997.51	4 846	1087.73
<i>Helleborus foetidus</i>	ubiquitous	grassy	2 881	51.48	2 372	18.62
<i>Hepatica nobilis</i>	mountainous	grassy	3 330	171.77	3 178	193.25
<i>Hieracium murorum</i>	ubiquitous	grassy	4 945	389.15	4 694	314.08
<i>Hieracium prenanthoides</i>	mountainous	grassy	1 259	287.54	1 343	448.85
<i>Holcus mollis</i>	ubiquitous	grassy	1 731	102.38	2 023	144.85
<i>Homogyne alpina</i>	mountainous	grassy	1 492	751.76	1 246	637.98
<i>Hordelymus europaeus</i>	mountainous	grassy	1 042	108.60	1 374	177.34
<i>Ilex aquifolium</i>	ubiquitous	woody	3 650	267.37	3 273	212.43
<i>Juniperus communis</i>	ubiquitous	woody	3 193	63.27	2 885	30.79
<i>Knautia dipsacifolia</i>	mountainous	grassy	986	45.18	572	50.65
<i>Lamium galeobdolon</i>	ubiquitous	grassy	2 969	121.59	3 230	95.01
<i>Laserpitium gallicum</i>	mountainous	grassy	639	39.87	664	37.52
<i>Laserpitium latifolium</i>	mountainous	grassy	1 132	87.64	920	135.18
<i>Lathyrus linifolius</i>	ubiquitous	grassy	1 754	47.65	1 880	101.72
<i>Lathyrus niger</i>	mountainous	grassy	623	54.26	546	28.16
<i>Lathyrus vernus</i>	mountainous	grassy	1 737	66.69	1 634	90.08
<i>Leucobryum glaucum</i>	ubiquitous	grassy	905	102.37	853	111.61
<i>Ligustrum vulgare</i>	ubiquitous	woody	2 532	211.76	2 155	260.63
<i>Lilium martagon</i>	mountainous	grassy	1 634	86.44	1 443	154.00
<i>Lonicera alpigena</i>	mountainous	woody	1 160	227.46	1 418	365.73
<i>Lonicera etrusca</i>	ubiquitous	woody	1 628	129.95	1 393	104.33
<i>Lonicera nigra</i>	mountainous	woody	1 831	461.77	2 501	613.27

Species	Range area	Life-form	1905-1985		1986-2005	
			D <sub>0</sub>	D <sub>0</sub> -D	D <sub>0</sub>	D <sub>0</sub> -D
<i>Lonicera periclymenum</i>	ubiquitous	woody	2 685	305.26	2 541	361.45
<i>Lonicera xylosteum</i>	ubiquitous	woody	3 262	242.35	2 992	153.83
<i>Luzula luzuloides</i>	mountainous	grassy	2 315	178.36	1 981	141.66
<i>Luzula nivea</i>	mountainous	grassy	2 496	451.97	2 937	820.05
<i>Lysimachia nemorum</i>	ubiquitous	grassy	1 253	88.17	807	21.67
<i>Maianthemum bifolium</i>	mountainous	grassy	1 737	150.89	1 292	140.78
<i>Melampyrum sylvaticum</i>	mountainous	grassy	1 754	567.27	1 285	384.28
<i>Melampyrum velebicum</i>	mountainous	grassy	1 213	142.48	949	127.04
<i>Melica uniflora</i>	ubiquitous	grassy	2 921	111.15	2 510	34.05
<i>Melittis melissophyllum</i>	ubiquitous	grassy	2 170	189.31	1 714	48.93
<i>Mercurialis perennis</i>	ubiquitous	grassy	2 795	174.27	2 634	159.59
<i>Milium effusum</i>	ubiquitous	grassy	2 315	34.58	2 074	45.67
<i>Moehringia trinervia</i>	ubiquitous	grassy	1 923	35.73	1 546	18.55
<i>Mycelis muralis</i>	ubiquitous	grassy	3 066	106.99	2 957	66.05
<i>Neottia nidus-avis</i>	ubiquitous	grassy	1 393	80.83	1 112	61.73
<i>Orthilia secunda</i>	mountainous	grassy	2 214	477.09	1 703	357.33
<i>Oxalis acetosella</i>	ubiquitous	grassy	4 268	306.31	4 162	384.18
<i>Paris quadrifolia</i>	ubiquitous	grassy	2 301	201.82	2 363	172.07
<i>Phyteuma ovatum</i>	mountainous	grassy	546	212.67	792	290.35
<i>Phyteuma spicatum</i>	ubiquitous	grassy	2 857	175.21	2 905	244.23
<i>Pimpinella saxifraga</i>	ubiquitous	grassy	631	52.87	563	22.01
<i>Pinus cembra</i>	mountainous	woody	589	281.25	1 021	633.54
<i>Pinus sylvestris</i>	mountainous	woody	3 302	109.36	3 096	118.90
<i>Poa nemoralis</i>	ubiquitous	grassy	3 663	45.72	3 534	26.18
<i>Polygala chamaebuxus</i>	mountainous	grassy	1 253	319.48	631	105.81
<i>Polygonatum multiflorum</i>	ubiquitous	grassy	1 896	94.99	1 869	136.47
<i>Polygonatum odoratum</i>	ubiquitous	grassy	1 842	130.09	1 021	53.33
<i>Polygonatum verticillatum</i>	mountainous	grassy	2 160	315.04	2 651	376.11
<i>Polypodium vulgare</i>	ubiquitous	grassy	2 334	48.82	2 099	34.83
<i>Polystichum aculeatum</i>	mountainous	grassy	838	28.32	1 173	102.23
<i>Prenanthes purpurea</i>	mountainous	grassy	4 338	596.87	4 157	773.12
<i>Primula elatior</i>	ubiquitous	grassy	1 035	23.07	1 220	32.42
<i>Prunus avium</i>	ubiquitous	woody	2 272	51.27	2 550	159.53
<i>Prunus mahaleb</i>	ubiquitous	woody	1 132	49.78	1 480	75.68
<i>Prunus spinosa</i>	ubiquitous	woody	2 038	102.51	2 234	126.62
<i>Pteridium aquilinum</i>	ubiquitous	grassy	4 094	339.78	3 866	451.63
<i>Pulmonaria affinis</i>	ubiquitous	grassy	868	35.01	1 587	35.59
<i>Pulsatilla alpina</i>	mountainous	grassy	555	197.37	964	490.82
<i>Quercus petraea</i>	ubiquitous	woody	3 641	258.75	3 330	382.91
<i>Quercus pubescens</i>	ubiquitous	woody	3 983	236.21	3 851	240.46
<i>Quercus robur</i>	ubiquitous	woody	2 836	363.76	2 301	344.67
<i>Ranunculus aduncus</i>	mountainous	grassy	823	98.18	1 657	316.07
<i>Rhamnus cathartica</i>	ubiquitous	woody	927	64.36	606	17.25
<i>Ribes alpinum</i>	mountainous	woody	1 674	117.12	2 301	137.12
<i>Ribes petraeum</i>	mountainous	woody	737	60.11	913	143.13
<i>Rosa arvensis</i>	ubiquitous	woody	1 272	48.45	2 094	114.67
<i>Rosa canina</i>	ubiquitous	woody	1 473	77.28	2 358	74.90
<i>Rosa pendulina</i>	mountainous	woody	1 640	392.74	2 048	569.51
<i>Rubus fruticosus</i>	ubiquitous	woody	737	55.51	2 677	144.05
<i>Rubus idaeus</i>	mountainous	woody	3 251	384.90	3 208	465.86
<i>Rubus saxatilis</i>	mountainous	woody	942	204.44	993	163.33
<i>Rumex arifolius</i>	mountainous	grassy	689	128.97	942	229.65
<i>Salix caprea</i>	ubiquitous	woody	784	21.25	1 021	36.48

Species	Range area	Life-form	1905-1985		1986-2005	
			D <sub>0</sub>	D <sub>0</sub> -D	D <sub>0</sub>	D <sub>0</sub> -D
<i>Sambucus racemosa</i>	mountainous	woody	2 315	116.06	1 981	154.67
<i>Sanicula europaea</i>	ubiquitous	grassy	1 776	35.68	1 965	111.54
<i>Saxifraga cuneifolia</i>	mountainous	grassy	942	270.43	935	129.40
<i>Saxifraga rotundifolia</i>	mountainous	grassy	913	192.33	1 139	261.06
<i>Scilla lilio-hyacinthus</i>	mountainous	grassy	648	85.01	555	58.76
<i>Senecio ovatus subsp. ovatus</i>	mountainous	grassy	1 467	95.90	1 725	55.01
<i>Solidago virgaurea</i>	ubiquitous	grassy	1 896	42.94	2 189	97.13
<i>Sorbus aria</i>	mountainous	woody	4 203	472.73	4 139	363.09
<i>Sorbus aucuparia</i>	mountainous	woody	4 253	505.73	4 465	778.28
<i>Sorbus torminalis</i>	ubiquitous	woody	1 070	141.21	729	53.63
<i>Stellaria nemorum</i>	mountainous	grassy	1 510	116.68	1 599	138.46
<i>Tamus communis</i>	ubiquitous	grassy	2 135	210.08	1 885	222.43
<i>Teucrium scorodonia</i>	ubiquitous	grassy	3 193	191.99	3 534	364.42
<i>Tilia platyphyllos</i>	ubiquitous	woody	1 510	140.32	1 725	90.79
<i>Trifolium ochroleucon</i>	ubiquitous	grassy	689	48.27	964	25.63
<i>Ulmus glabra</i>	mountainous	woody	890	54.26	1 077	28.68
<i>Valeriana montana</i>	mountainous	grassy	883	202.91	639	124.83
<i>Veratrum album</i>	mountainous	grassy	639	168.68	905	203.38
<i>Veronica austriaca</i>	ubiquitous	grassy	1 387	368.18	1 430	388.96
<i>Veronica officinalis</i>	ubiquitous	grassy	2 559	187.93	2 311	126.08
<i>Viburnum lantana</i>	ubiquitous	woody	2 857	159.97	2 414	123.19
<i>Viburnum opulus</i>	ubiquitous	woody	1 233	77.84	1 200	90.45
<i>Vicia sepium</i>	ubiquitous	grassy	2 703	88.16	2 651	52.24
<i>Vincetoxicum hirundinaria</i>	ubiquitous	grassy	1 368	28.95	1 455	44.86
<i>Viola biflora</i>	mountainous	grassy	721	265.12	729	243.60
<i>Viola hirta</i>	ubiquitous	grassy	1 220	48.83	768	47.04
<i>Viola reichenbachiana</i>	ubiquitous	grassy	4 326	140.95	4 297	136.68



**Table S2.** Magnitude of shift, optimum elevation (OPT) and 95% confidence interval (INF.CI and SUP.CI) around each species optimum elevation for both periods (1905-1985 and 1986-2005). Species in bold show non-overlapping 95% confidence interval between periods. Species nomenclature followed Flora Europaea (S16).

Species	Shift (m)	1905-1985			1986-2005		
		INF.CI	OPT (m)	SUP.CI	INF.CI	OPT (m)	SUP.CI
<i>Abies alba</i>	214	1 174	1 214	1 261	1 380	1 428	1 486
<i>Acer campestre</i>	18	563	642	702	596	660	710
<b><i>Acer monspessulanum</i></b>	<b>139</b>	<b>551</b>	<b>597</b>	<b>639</b>	<b>664</b>	<b>736</b>	<b>802</b>
<b><i>Acer opalus</i></b>	<b>137</b>	<b>853</b>	<b>899</b>	<b>948</b>	<b>986</b>	<b>1 035</b>	<b>1 093</b>
<i>Acer platanoides</i>	124	704	790	876	808	914	1 022
<b><i>Acer pseudoplatanus</i></b>	<b>137</b>	<b>988</b>	<b>1 042</b>	<b>1 104</b>	<b>1 125</b>	<b>1 178</b>	<b>1 244</b>
<b><i>Actaea spicata</i></b>	<b>230</b>	<b>1 109</b>	<b>1 169</b>	<b>1 249</b>	<b>1 338</b>	<b>1 398</b>	<b>1 481</b>
<i>Adenostyles alliariae</i>	126	1 526	1 654	1 916	1 666	1 780	1 984
<i>Anemone nemorosa</i>	-57	587	784	910	438	728	863
<i>Anthyllis vulneraria</i>	-187	1 399	1 596	2 240	1 282	1 409	1 679
<i>Aquilegia vulgaris</i>	22	1 353	1 549	2 136	1 422	1 571	1 926
<i>Arabis turrita</i>	204	783	853	934	926	1 056	1 263
<b><i>Aruncus dioicus</i></b>	<b>253</b>	<b>1 108</b>	<b>1 180</b>	<b>1 286</b>	<b>1 317</b>	<b>1 433</b>	<b>1 670</b>
<i>Aster bellidiastrum</i>	-60	1 790	2 016	2 779	1 823	1 956	2 296
<i>Athyrium filix-femina</i>	-12	1 076	1 135	1 209	1 069	1 123	1 190
<i>Atrichum undulatum</i>	16	66	492	626	95	508	652
<i>Berberis vulgaris</i>	116	1 460	1 606	1 915	1 537	1 722	2 244
<i>Blechnum spicant</i>	-344	1 222	1 389	1 836	915	1 045	1 236
<b><i>Buxus sempervirens</i></b>	<b>165</b>	<b>751</b>	<b>780</b>	<b>810</b>	<b>860</b>	<b>946</b>	<b>1 032</b>
<i>Calamagrostis varia</i>	-94	1 624	1 732	1 939	1 536	1 638	1 831
<i>Calamintha grandiflora</i>	50	1 362	1 417	1 491	1 429	1 467	1 515
<i>Campanula rhomboidalis</i>	-165	1 715	1 872	2 319	1 619	1 707	1 888
<i>Campanula rotundifolia</i>	-199	1 403	1 498	1 650	1 207	1 299	1 450
<b><i>Cardamine heptaphylla</i></b>	<b>173</b>	<b>1 073</b>	<b>1 120</b>	<b>1 178</b>	<b>1 244</b>	<b>1 293</b>	<b>1 356</b>
<b><i>Cardamine pentaphyllos</i></b>	<b>224</b>	<b>1 204</b>	<b>1 289</b>	<b>1 426</b>	<b>1 450</b>	<b>1 513</b>	<b>1 607</b>
<i>Cardamine pratensis</i>	105	318	486	575	402	590	686
<b><i>Carex digitata</i></b>	<b>251</b>	<b>922</b>	<b>1 013</b>	<b>1 129</b>	<b>1 168</b>	<b>1 264</b>	<b>1 420</b>
<i>Carex sylvatica</i>	8	528	749	878	649	757	837
<i>Carpinus betulus</i>	67	321	379	421	412	446	473
<i>Castanea sativa</i>	26	442	475	502	452	500	537
<b><i>Cephalanthera longifolia</i></b>	<b>495</b>	<b>255</b>	<b>647</b>	<b>800</b>	<b>1 058</b>	<b>1 142</b>	<b>1 264</b>
<i>Cephalanthera rubra</i>	68	808	913	1 027	879	981	1 111
<i>Cicerbita alpina</i>	73	1 501	1 612	1 840	1 562	1 684	1 966
<b><i>Clinopodium vulgare</i></b>	<b>-377</b>	<b>569</b>	<b>693</b>	<b>780</b>	<b>-419</b>	<b>317</b>	<b>521</b>
<i>Corylus avellana</i>	38	667	722	768	717	760	798
<i>Crataegus laevigata</i>	65	123	510	643	479	575	640
<i>Crataegus monogyna</i>	-62	318	436	514	128	374	503
<i>Cruciata glabra</i>	-112	1 395	1 531	1 812	1 291	1 419	1 687
<i>Cytisophyllum sessilifolium</i>	17	546	672	758	-272	689	891
<i>Cytisus scoparius</i>	-14	539	612	668	552	598	636
<i>Dactylorhiza maculata</i>	14	1 234	1 393	1 818	1 316	1 407	1 556
<b><i>Daphne laureola</i></b>	<b>170</b>	<b>737</b>	<b>812</b>	<b>880</b>	<b>929</b>	<b>982</b>	<b>1 040</b>
<i>Digitalis lutea</i>	147	666	837	979	883	984	1 105
<i>Digitalis purpurea</i>	-73	935	994	1 063	843	921	1 005
<b><i>Dryopteris dilatata</i></b>	<b>-235</b>	<b>1 111</b>	<b>1 193</b>	<b>1 313</b>	<b>913</b>	<b>958</b>	<b>1 006</b>

Species	Shift (m)	1905-1985			1986-2005		
		INF.CI	OPT (m)	SUP.CI	INF.CI	OPT (m)	SUP.CI
<i>Dryopteris filix-mas</i>	26	1 126	1 197	1 293	1 173	1 223	1 287
<i>Epilobium angustifolium</i>	-175	1 552	1 710	2 041	1 417	1 535	1 751
<b><i>Epilobium montanum</i></b>	<b>211</b>	<b>1 137</b>	<b>1 193</b>	<b>1 265</b>	<b>1 347</b>	<b>1 405</b>	<b>1 480</b>
<i>Epipactis atrorubens</i>	233	1 348	1 464	1 679	1 540	1 696	2 092
<i>Epipactis helleborine</i>	70	789	915	1 042	879	985	1 102
<i>Euphorbia characias</i>	213	-793	50	214	-170	263	378
<i>Evonymus europaeus</i>	141	71	294	384	318	435	498
<b><i>Fagus sylvatica</i></b>	<b>121</b>	<b>942</b>	<b>962</b>	<b>983</b>	<b>1 061</b>	<b>1 083</b>	<b>1 107</b>
<b><i>Festuca altissima</i></b>	<b>239</b>	<b>778</b>	<b>824</b>	<b>870</b>	<b>1 014</b>	<b>1 062</b>	<b>1 120</b>
<b><i>Festuca flavesceus</i></b>	<b>524</b>	<b>1 805</b>	<b>1 891</b>	<b>2 070</b>	<b>2 129</b>	<b>2 415</b>	<b>3 356</b>
<i>Festuca heterophylla</i>	-98	899	972	1 055	809	874	934
<i>Fragaria vesca</i>	54	1 140	1 205	1 290	1 182	1 259	1 368
<i>Fraxinus excelsior</i>	27	752	803	851	784	830	873
<b><i>Galeopsis tetrahit</i></b>	<b>198</b>	<b>611</b>	<b>740</b>	<b>832</b>	<b>874</b>	<b>938</b>	<b>1 006</b>
<b><i>Galium odoratum</i></b>	<b>116</b>	<b>1 074</b>	<b>1 108</b>	<b>1 148</b>	<b>1 186</b>	<b>1 225</b>	<b>1 270</b>
<b><i>Galium rotundifolium</i></b>	<b>257</b>	<b>1 072</b>	<b>1 150</b>	<b>1 260</b>	<b>1 334</b>	<b>1 406</b>	<b>1 510</b>
<i>Galium saxatile</i>	-77	1 021	1 095	1 197	963	1 018	1 085
<i>Genista cinerea</i>	218	864	936	1 027	1 015	1 153	1 422
<i>Genista pilosa</i>	-169	694	805	897	350	636	761
<i>Gentiana lutea</i>	149	1 652	1 760	1 960	1 809	1 909	2 106
<i>Geranium nodosum</i>	85	1 098	1 289	1 983	1 304	1 374	1 475
<i>Geranium robertianum</i>	66	957	1 013	1 077	1 028	1 079	1 139
<i>Gymnocarpium dryopteris</i>	196	1 443	1 533	1 678	1 556	1 729	2 209
<i>Hedera helix</i>	-80	97	222	304	-70	142	265
<i>Helleborus foetidus</i>	-97	768	855	932	370	757	914
<i>Hepatica nobilis</i>	498	1 396	1 529	1 766	1 705	2 028	2 984
<i>Hieracium murorum</i>	162	1 303	1 366	1 448	1 429	1 528	1 677
<i>Hieracium prenanthoides</i>	-259	1 897	2 176	2 988	1 820	1 917	2 095
<i>Holcus mollis</i>	-121	-30	349	492	-418	228	428
<i>Homogyne alpina</i>	-215	2 090	2 337	3 180	2 018	2 122	2 332
<b><i>Hordelymus europaeus</i></b>	<b>196</b>	<b>1 044</b>	<b>1 099</b>	<b>1 170</b>	<b>1 240</b>	<b>1 295</b>	<b>1 367</b>
<i>Ilex aquifolium</i>	-10	684	722	756	663	712	753
<i>Juniperus communis</i>	-148	1 259	1 419	1 779	1 134	1 271	1 559
<i>Knautia dipsacifolia</i>	200	1 137	1 249	1 451	1 317	1 449	1 751
<i>Lamium galeobdolon</i>	39	856	904	954	889	943	997
<i>Laserpitium gallicum</i>	-67	1 335	1 538	2 303	1 300	1 471	1 992
<i>Laserpitium latifolium</i>	321	1 305	1 419	1 626	1 590	1 740	2 074
<b><i>Lathyrus linifolius</i></b>	<b>149</b>	<b>846</b>	<b>923</b>	<b>1 007</b>	<b>1 018</b>	<b>1 072</b>	<b>1 139</b>
<i>Lathyrus niger</i>	138	607	676	748	711	814	920
<b><i>Lathyrus vernus</i></b>	<b>351</b>	<b>1 086</b>	<b>1 168</b>	<b>1 287</b>	<b>1 376</b>	<b>1 519</b>	<b>1 819</b>
<i>Leucobryum glaucum</i>	19	93	318	404	84	337	424
<i>Ligustrum vulgare</i>	-317	247	394	480	-616	77	288
<i>Lilium martagon</i>	23	1 415	1 609	2 107	1 501	1 632	1 880
<i>Lonicera alpigena</i>	-119	1 653	1 790	2 060	1 605	1 670	1 767
<i>Lonicera etrusca</i>	-5	450	531	589	392	526	602
<i>Lonicera nigra</i>	4	1 529	1 586	1 663	1 537	1 590	1 660
<i>Lonicera periclymenum</i>	9	275	379	444	289	388	449
<i>Lonicera xylosteum</i>	36	944	979	1 016	972	1 014	1 061
<b><i>Luzula luzuloides</i></b>	<b>190</b>	<b>443</b>	<b>525</b>	<b>583</b>	<b>665</b>	<b>715</b>	<b>759</b>
<i>Luzula nivea</i>	115	1 415	1 471	1 545	1 541	1 587	1 644
<i>Lysimachia nemorum</i>	-7	1 127	1 202	1 308	1 060	1 194	1 470
<i>Maianthemum bifolium</i>	59	1 260	1 336	1 446	1 318	1 394	1 509
<i>Melampyrum sylvaticum</i>	380	1 774	1 874	2 043	2 006	2 254	2 933

Species	Shift (m)	1905-1985			1986-2005		
		INF.CI	OPT (m)	SUP.CI	INF.CI	OPT (m)	SUP.CI
<i>Melampyrum velebaticum</i>	-21	1 257	1 328	1 430	1 244	1 307	1 395
<b>Melica uniflora</b>	<b>249</b>	<b>540</b>	<b>640</b>	<b>711</b>	<b>778</b>	<b>890</b>	<b>985</b>
<i>Melittis melissophyllum</i>	167	631	672	711	751	839	917
<i>Mercurialis perennis</i>	126	844	882	922	967	1 008	1 053
<i>Milium effusum</i>	412	834	931	1 032	1 209	1 343	1 624
<i>Moehringia trinervia</i>	227	745	851	945	949	1 078	1 267
<i>Mycelis muralis</i>	117	1 001	1 056	1 121	1 095	1 173	1 281
<i>Neottia nidus-avis</i>	156	1 017	1 082	1 167	1 150	1 238	1 374
<i>Orthilia secunda</i>	167	1 530	1 598	1 693	1 661	1 766	1 939
<i>Oxalis acetosella</i>	-6	1 396	1 492	1 636	1 410	1 486	1 591
<i>Paris quadrifolia</i>	35	1 175	1 229	1 298	1 206	1 264	1 341
<b>Phyteuma ovatum</b>	<b>258</b>	<b>1 785</b>	<b>1 840</b>	<b>1 936</b>	<b>1 949</b>	<b>2 097</b>	<b>2 512</b>
<b>Phyteuma spicatum</b>	<b>273</b>	<b>1 165</b>	<b>1 224</b>	<b>1 302</b>	<b>1 408</b>	<b>1 498</b>	<b>1 633</b>
<i>Pimpinella saxifraga</i>	-106	1 196	1 303	1 498	1 064	1 197	1 479
<i>Pinus cembra</i>	118	1 985	2 095	2 400	2 114	2 213	2 418
<i>Pinus sylvestris</i>	-12	1 067	1 128	1 206	1 063	1 116	1 180
<i>Poa nemoralis</i>	-128	1 073	1 175	1 334	940	1 047	1 175
<i>Polygala chamaebuxus</i>	90	1 621	1 700	1 827	1 626	1 791	2 248
<i>Polygonatum multiflorum</i>	-46	466	581	657	416	535	607
<b>Polygonatum odoratum</b>	<b>146</b>	<b>853</b>	<b>897</b>	<b>944</b>	<b>973</b>	<b>1 043</b>	<b>1 133</b>
<i>Polygonatum verticillatum</i>	41	1 206	1 249	1 301	1 249	1 289	1 338
<b>Polypodium vulgare</b>	<b>292</b>	<b>883</b>	<b>961</b>	<b>1 048</b>	<b>1 129</b>	<b>1 253</b>	<b>1 488</b>
<i>Polystichum aculeatum</i>	90	1 022	1 137	1 338	1 162	1 228	1 320
<i>Prenanthes purpurea</i>	53	1 307	1 351	1 405	1 365	1 404	1 450
<i>Primula elatior</i>	-158	648	799	921	322	642	773
<i>Prunus avium</i>	-28	-222	434	628	139	406	531
<i>Prunus mahaleb</i>	-31	671	757	836	648	725	789
<b>Prunus spinosa</b>	<b>189</b>	<b>257</b>	<b>468</b>	<b>575</b>	<b>578</b>	<b>657</b>	<b>715</b>
<i>Pteridium aquilinum</i>	-102	338	446	519	184	344	439
<i>Pulmonaria affinis</i>	-22	1 043	1 149	1 325	1 031	1 127	1 268
<i>Pulsatilla alpina</i>	163	1 806	1 889	2 084	1 978	2 053	2 194
<i>Quercus petraea</i>	-62	587	637	679	529	575	611
<b>Quercus pubescens</b>	<b>-347</b>	<b>434</b>	<b>534</b>	<b>603</b>	<b>-355</b>	<b>187</b>	<b>401</b>
<i>Quercus robur</i>	-76	255	354	417	90	278	371
<i>Ranunculus aduncus</i>	65	1 453	1 593	1 895	1 571	1 657	1 791
<i>Rhamnus cathartica</i>	123	716	779	846	761	903	1 057
<i>Ribes alpinum</i>	94	1 046	1 101	1 172	1 139	1 196	1 270
<i>Ribes petraeum</i>	264	1 266	1 386	1 624	1 535	1 650	1 875
<i>Rosa arvensis</i>	83	510	650	742	672	733	785
<i>Rosa canina</i>	50	820	878	940	867	928	989
<i>Rosa pendulina</i>	-14	1 622	1 708	1 841	1 632	1 694	1 782
<b>Rubus fruticosus</b>	<b>-231</b>	<b>812</b>	<b>877</b>	<b>953</b>	<b>561</b>	<b>646</b>	<b>706</b>
<i>Rubus idaeus</i>	55	1 334	1 392	1 468	1 393	1 447	1 516
<i>Rubus saxatilis</i>	-74	1 527	1 605	1 730	1 451	1 531	1 661
<i>Rumex arifolius</i>	341	1 695	1 901	2 563	1 951	2 242	3 293
<i>Salix caprea</i>	-78	1 041	1 183	1 491	1 012	1 104	1 239
<i>Sambucus racemosa</i>	9	1 214	1 299	1 426	1 241	1 308	1 400
<b>Sanicula europaea</b>	<b>315</b>	<b>843</b>	<b>935</b>	<b>1 035</b>	<b>1 180</b>	<b>1 250</b>	<b>1 347</b>
<b>Saxifraga cuneifolia</b>	<b>-236</b>	<b>1 660</b>	<b>1 732</b>	<b>1 856</b>	<b>1 408</b>	<b>1 497</b>	<b>1 645</b>
<i>Saxifraga rotundifolia</i>	97	1 530	1 613	1 749	1 624	1 710	1 856
<i>Scilla lilio-hyacinthus</i>	117	1 228	1 308	1 435	1 313	1 425	1 650
<b>Senecio ovatus subsp. ovatus</b>	<b>300</b>	<b>805</b>	<b>856</b>	<b>911</b>	<b>1 074</b>	<b>1 156</b>	<b>1 271</b>
<i>Solidago virgaurea</i>	-30	1 129	1 250	1 473	1 148	1 219	1 317

Species	Shift (m)	1905-1985			1986-2005		
		INF.CI	OPT (m)	SUP.CI	INF.CI	OPT (m)	SUP.CI
<b><i>Sorbus aria</i></b>	<b>79</b>	<b>1 017</b>	<b>1 044</b>	<b>1 073</b>	<b>1 091</b>	<b>1 123</b>	<b>1 158</b>
<i>Sorbus aucuparia</i>	54	1 532	1 641	1 805	1 602	1 695	1 825
<i>Sorbus torminalis</i>	-14	521	559	596	375	545	632
<b><i>Stellaria nemorum</i></b>	<b>229</b>	<b>1 159</b>	<b>1 228</b>	<b>1 324</b>	<b>1 362</b>	<b>1 457</b>	<b>1 613</b>
<i>Tamus communis</i>	-166	-244	176	334	-1 099	10	265
<i>Teucrium scorodonia</i>	74	364	490	570	507	564	607
<i>Tilia platyphyllos</i>	48	651	694	736	676	742	798
<i>Trifolium ochroleucon</i>	41	764	835	916	760	876	986
<i>Ulmus glabra</i>	11	769	837	911	732	848	951
<i>Valeriana montana</i>	82	1 648	1 758	1 973	1 680	1 840	2 297
<i>Veratrum album</i>	188	1 720	1 840	2 155	1 824	2 028	2 604
<i>Veronica austriaca</i>	73	1 532	1 586	1 661	1 601	1 660	1 744
<i>Veronica officinalis</i>	55	1 409	1 527	1 727	1 432	1 582	1 885
<i>Viburnum lantana</i>	79	900	941	985	973	1 019	1 072
<i>Viburnum opulus</i>	-24	308	482	574	224	458	558
<i>Vicia sepium</i>	75	969	1 028	1 098	1 026	1 103	1 203
<b><i>Vincetoxicum hirundinaria</i></b>	<b>198</b>	<b>788</b>	<b>896</b>	<b>1 007</b>	<b>1 011</b>	<b>1 094</b>	<b>1 207</b>
<b><i>Viola biflora</i></b>	<b>213</b>	<b>1 730</b>	<b>1 781</b>	<b>1 864</b>	<b>1 869</b>	<b>1 994</b>	<b>2 317</b>
<b><i>Viola hirta</i></b>	<b>189</b>	<b>525</b>	<b>656</b>	<b>745</b>	<b>773</b>	<b>845</b>	<b>922</b>
<b><i>Viola reichenbachiana</i></b>	<b>157</b>	<b>1 043</b>	<b>1 095</b>	<b>1 156</b>	<b>1 184</b>	<b>1 252</b>	<b>1 343</b>

## References

- S1. J. C. Gégout, C. Coudun, G. Bailly, B. Jabiol, *Journal of Vegetation Science* **16**, 257 (2005).
- S2. H. Brisse, P. de Ruffray, G. Grandjouan, M. Hoff, *Annali di botanica* **53**, 177 (1995).
- S3. P. D. Jones, T. J. Osborn, K. R. Briffa, *Science* **292**, 662 (2001).
- S4. L. P. Shoo, S. E. Williams, J. M. Hero, *Austral Ecology* **31**, 22 (2006).
- S5. P. Benichou, O. Le Breton, *La Météorologie* **19**, 23 (1987).
- S6. C. J. F. ter Braak, C. W. N. Looman, *Vegetatio* **65**, 3 (1986).
- S7. P. McCullagh, J. A. Nelder, Generalized linear models, Monographs on Statistics and Applied Probability (Chapman & Hall, London, UK, ed. Reprinted, 1997).
- S8. C. J. F. ter Braak, L. G. Barendregt, *Mathematical Biosciences* **78**, 57 (1986).
- S9. C. Coudun, J.-C. Gégout, *Ecological Modelling* **199**, 164 (2006).
- S10. M. P. Austin, A. O. Nicholls, *Journal of Vegetation Science* **8**, 743 (1997).
- S11. T. J. Hastie, R. J. Tibshirani, Generalized additive models (Chapman & Hall, London, UK, 1990).
- S12. J. Oksanen, E. Läärä, K. Tolonen, B. G. Warner, *Ecology* **82**, 1191 (2001).
- S13. J.-C. Rameau, D. Mansion, G. Dumé, *Flore forestière française. Guide écologique illustré. Tome 1 : plaines et collines* (Institut pour le Développement, Paris, 1989).
- S14. J.-C. Rameau, D. Mansion, G. Dumé, *Flore forestière française. Guide écologique illustré. Tome 2 : montagnes* (Institut pour le Développement, Paris, 1993).



- S15. H. Ellenberg, H.E. Weber, R. Düll, V. Wirth, W. Werner, D. Paulißen, *Scripta Geobotanica* **18**, 1 (1992).
- S16. T. G. Tutin, V.H. Heywood, N.A. Burges, D.H. Valentine, S.M. Walters, D.A. Webb, *Flora Europaea. Volume 5 set* (Cambridge University Press, 2001).

## Fahrausweisentzug wird grenzüberschreitend

*Britisch-irische Einigung als Exempel*

*ali. Dublin, 26. Juni*

Britische, nordirische und irische Minister haben am Donnerstag in Belfast ein Abkommen unterschrieben, das den Entzug des Fahrausweises in einer Jurisdiktion für alle verbindlich macht. Die Vereinbarung wird im nächsten März in Kraft treten. Sie stützt sich auf eine entsprechende europäische Konvention aus dem Jahre 1998, die aber bisher noch nirgends umgesetzt wurde. Die Minister bekräftigten ferner ihre Absicht, auch die nationalen Systeme der Strafpunkte für fehlbare Autolenker zu harmonisieren, räumten aber ein, dass dieses Vorhaben technisch weit komplexer sei.

Das grenzüberschreitende Vorgehen gegen skrupellose Autofahrer wird nach Ansicht des irischen Transportministers, Noel Dempsey, in erster Linie der Grenzregion zwischen Irland und Nordirland zugutekommen. Er wies darauf hin, dass die Zahl der Verkehrstoten und -verletzten entlang der Grenze um ein Drittel höher liege als die jeweiligen nationalen Durchschnitte. Das liege vor allem daran, meinte Dempsey, dass Fahrer ausserhalb ihres eigenen Landes meinten, sie stünden über dem Recht. Die Diskrepanz mag indessen auch etwas mit der bescheidenen Qualität dieser abgelegenen Landsträsschen zu tun haben.

## Mann im Aargau bei der Verhaftung erstickt

*Medizinisches Gutachten belastet Polizei*

(ap) Eine tödlich ausgegangene Polizeiintervention im aargauischen Fislisbach dürfte zur Anklage gegen zwei Beamte führen. Wie Untersuchungsrichter Beat Richner am Donnerstag mitteilte, hatten diese einen psychisch Angeschlagenen mit zusammengebandenen Armen niedergedrückt, worauf der 41-Jährige erstickte.

Die zwei Regionalpolizisten wollten am frühen Morgen des 11. Septembers 2007 in Fislisbach einen psychisch angeschlagenen Mann ins Kantonsspital überführen. Er hatte seine Medikamente nicht eingenommen. Nach verbaler Gegenwehr stürzte sich der Mann aus dem Küchenfenster des ersten Stockes drei Meter in die Tiefe. Im Garten stellte er sich den Beamten mit einem Brett entgegen, liess dieses aber unter vorgehaltener Waffe fallen, worauf es zu einer mehrere Minuten dauernden handfesten Auseinandersetzung kam. Der Mann wurde schliesslich in Bauchlage mit auf dem Rücken gefesselten Händen fixiert. Als kurz darauf die alarmierte Ambulanz eintraf, war der Mann bereits tot.

Ein provisorisches medizinisches Gutachten stellte fest, dass der Tod durch ein «lagebedingtes Erstickten» eingetreten war, also ein klarer Zusammenhang zwischen Tod und Polizeieinsatz besteht. Nach Abschluss der Untersuchung werde nun durch das Bezirksamt Baden ein Schlussbericht zur Anklage an die Aargauer Staatsanwaltschaft verfasst. Richner geht davon aus, dass Letztere dann Anklage erhebt.

## Mit mehr Schub zum Mond

*Nasa präsentiert neue Rakete «Ares V»*

Huntsville, 26. Juni. (ap) Die amerikanische Raumfahrtbehörde Nasa hat eine neue Version der geplanten Rakete «Ares V» vorgestellt, die im Jahr 2020 Astronauten zum Mond bringen soll. Die Rakete wird demnach sechs Meter länger werden und eine grössere Nutzlast ins All bringen können als zunächst geplant. Dazu bekommt sie sechs statt fünf Starttriebwerke. Und auch die beiden zusätzlichen Feststoffraketen an der Seite werden grösser ausfallen, wie Steve Cook, der Manager des Ares-Projektbüros im Raumfahrtzentrum Marshall in Huntsville, Alabama, am Mittwoch Ortszeit sagte.

Ursprünglich sollte die «Ares V» rund 110 Meter hoch werden, was ungefähr den Massen der ersten Mondrakete, «Saturn V», entspricht. Die neue «Ares V»-Version wird nun 116 Meter hoch. Sie soll vier Astronauten, eine Landefähre und anderes Gerät transportieren können. Insgesamt liegt die Nutzlast, die zum Mond und später vielleicht auch einmal zum Mars gebracht werden kann, bei über 71 Tonnen.

## 400 Verhaftungen bei Schlag gegen US-Pädophilenring

Washington, 26. Juni. (app) Die Polizei hat in den USA in einer mehrtägigen Aktion gegen einen Pädophilenring knapp 400 Verdächtige festgenommen. Während des fünftägigen Einsatzes in 16 Städten seien Hunderte von Polizeibeamten in verschiedenen Bundesstaaten zum Einsatz gekommen, berichtete die «New York Times» am Donnerstag. Es seien 389 Verdächtige festgenommen worden. Diese hätten zu einem Pädophilenring gehört, der mit verschwundenen und obdachlosen Minderjährigen handle. Insgesamt seien durch den Einsatz 433 missbrauchte Kinder gerettet worden.



In Leeuwarden rasen die Solarboote mit bis zu 30 km/h lautlos durch die Kanäle.

PETER DEJONG / AP

## Mit dem Solarboot durch die Niederlande

*40 Boote an der Regatta «Frisian Solar Challenge»*

Zum zweiten Mal wird in Friesland ein Solarbootrennen ausgetragen. Zu den Favoriten gehört das Team der Technischen Universität Delft. Unter den Teilnehmern befindet sich auch eine Mannschaft aus Brasilien, die ein Boot zur Beseitigung von Müll entwickelt hat.

*vau. Amsterdam, 26. Juni*

In den Niederlanden hat diese Woche das weltweit grösste Rennen für Solarboote begonnen. Den Startschuss für die Regatta «Frisian Solar Challenge» gab am Montag in der friesischen Provinzhauptstadt Leeuwarden die Wirtschaftsministerin Maria van der Hoeven. Bereits am Sonntag mussten die zahlreichen Teams aus den Benelux-Ländern, aus Grossbritannien, Deutschland, Schweden, Polen und Brasilien die Tauglichkeit ihrer selbstentwickelten und mit Sonnenenergie betriebenen Boote unter Beweis stellen. Um sich für die sechstägige, weltweit einzigartige Herausforderung zu qualifizieren, musste im Rahmen eines Prologs unter anderem auf einer Strecke von 10 Kilometern eine Mindestgeschwindigkeit von 8 km/h erreicht werden. Die Tour über insgesamt 220 Kilometer führt über Flüsse, Seen und Kanäle entlang elf friesischer Städte und wird am Samstag in Leeuwarden enden. Im Winter wird auf dieser Strecke jeweils der bekannteste niederländische Eisschnelllauf-Wettbewerb auf Natureis ausgetragen.

### Viele technische Hochschulen am Start

Wie bereits bei der ersten Austragung 2006 befinden sich unter den Teilnehmern viele Studenten, die einem technischen Studiengang folgen und von grossen Betrieben wie Banken und Versicherungen gesponsert werden. Unterschieden wird zwischen drei Klassen: Boote der A-Klasse sind mit einer Person, diejenigen der B-Klasse mit zwei Teilnehmern besetzt. In der sogenannten Offenen Klasse kann die Mannschaft selber bestimmen, wie viele Mitfahrende den Steuermann unterstützen. Wer an den Rennen teilnimmt, muss über ein Körpergewicht von mindestens 70 Kilogramm verfügen. Da während der Tour viele kleinere Brücken passiert werden müssen, ist es erlaubt, Breite und Höhe der Boote anzupassen. Falls notwendig dürfen die Boote – je nach Kategorie – von maximal fünf Personen (B-Klasse) für eine kurze Strecke aus dem Wasser gehievt werden.

Für die Teilnehmer wurden extra die Geschwindigkeitsbeschränkungen auf den engen Wasserwegen aufgehoben. Das Team der renommierten Technischen Universität Delft, das das

## Waadtländer Polizei hebt Drogenhändlerring aus

Lausanne, 26. Juni. (sda) Die Waadtländer Kantonspolizei hat einen Drogenhändlerring ausgehoben und 30 Personen, hauptsächlich aus Afrika, festgenommen. Im Zeitraum von zehn Monaten konnten insgesamt 21 Kilogramm Kokain sichergestellt werden. Die Ermittlungen ergaben, dass zwei grosse Drogenfunde am Flughafen Genf in einem Zusammenhang standen, wie die Polizei in einer Mitteilung vom Donnerstag schreibt. Im Juli 2007 hatten die Zollbehörden im doppelten Boden des Koffers einer Kamerunerin 10,3 Kilogramm Kokain aufgespürt. Der Empfänger der Droge ging der Polizei ebenfalls ins Netz. Im Oktober erwischte die Polizei in Yverdon-les-Bains einen Togolesen mit 8,3 Kilogramm Kokain im Gepäck. Zwei seiner Komplizen wurden ebenfalls festgenommen. Im November stellte die Polizei einen Berner Händler von Occasionsfahrzeugen und mutmasslichen Geldwäscher. Die internationalen Ermittlungen führten die Polizei nach Frankreich, Belgien, Deutschland und Österreich und betrafen mehrere Schweizer Kantone.

## Die Wärme treibt Pflanzen in höher gelegene Gebiete

(dpa) Der Klimawandel treibt die Pflanzen der westeuropäischen Wälder in immer höher gelegene Gebiete. Um den steigenden Temperaturen zu entkommen, sind die Pflanzen pro Jahrzehnt um durchschnittlich 29 Meter nach oben geklettert, wie ein französisch-chilenisches Forscherteam in der jüngsten Ausgabe der Fachzeitschrift «Science» berichtet. Die deutlichsten Höhenverschiebungen seien bei schnell wachsenden Pflanzenarten festzustellen sowie bei solchen, die ausschliesslich im Gebirge vorkommen.

Jonathan Lenoir vom Laboratoire d'Etude des Ressources Forêt-Bois in Nancy und seine Mitarbeiter hatten das Höhenvorkommen von 171 Pflanzenarten in sechs Waldgebieten Westeuropas untersucht, unter anderem in den Alpen, den Nordpyrenäen und den Vogesen. Sie untersuchten, in welcher Höhe sich die meisten Pflanzen einer Art im Zeitraum zwischen 1905 und 1985 fanden und in welcher Höhe zwischen 1986 und 2005. Insgesamt habe sich bei mehr als zwei Dritteln der untersuchten Arten der optimale Wuchstumsort gegen Ende des 20. und am Anfang des 21. Jahrhunderts nach oben verschoben.

Pflanzen mit ähnlichen ökologischen Ansprüchen zeigten dabei vergleichbare Höhenveränderungen. Die Wissenschaftler fanden in ihrer Untersuchung auch eine Bestätigung der Theorie, dass Pflanzen höher gelegener Gebiete besonders sensibel auf die Klimaerwärmung reagieren. Auch die Annahme, dass sich bei Gewächsen mit kurzem Generationswechsel stärkere Veränderungen feststellen lassen, bestätigte die Untersuchung. Für die Veränderungen seien mit grosser Wahrscheinlichkeit die steigenden Temperaturen infolge des Klimawandels verantwortlich, schreiben die Wissenschaftler. Andere Faktoren würden die Beobachtungen nicht erklären.

### KURZMELDUNGEN

**Polizisten schiessen in Südafrika auf Polizisten.** Südafrikanische Polizisten haben sich in Johannesburg eine heftige Schiesserei mit streikenden Kollegen geliefert. Mindestens sieben Polizisten wurden in der Nacht auf Donnerstag verletzt ins Spital gebracht, nachdem die von der Stadt angestellten protestierenden Ordnungshüter mit scharfer Munition auf ihre Kollegen gefeuert hatten. Diese wehrten sich mit Gummigeschossen. (dpa)

Anzeige



18-HOLE GOLF COURSE DESIGNED BY CABELL B. ROBINSON  
ROYAL PALM HOTEL  
ECO-CONSCIOUS DOMAIN  
LUXURIOUS SPA & SERVICES

BECOME A HOMEOWNER  
**+41 21 560 07 54**  
contact@domaineroyalpalm.com

**SALES OFFICE**  
IMMEUBLE BMCE, 3<sup>ÈME</sup> ÉTAGE,  
AV. MOHAMMED VI, MARRAKECH,  
MAROC

[www.domaineroyalpalm.com](http://www.domaineroyalpalm.com)

Photo: Philippe Levy - Atelier Vert Pomme - Illustrations are artists' depictions only and may differ from completed improvements, and scenes may include locations or activities not on the property. Improvements, facilities and programs are in formative stages, and there is no guarantee that they will be completed or developed. All pictures, photographs, and images are owned or licensed by Domaine Palm Marrakech S.A. or its affiliates. Any use, reproduction or distribution of pictures, photographs, and images without written permission is expressly prohibited.